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INTEROCULAR TRANSFER OF VISUAL DISCRIMINATION HABITS IN A TELEOST FISH[1]

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IN CONDUCTING experiments on the retention of visual discrimination habits following optic nerve transection and regeneration in teleosts, it became desirable to know whether habits learned with one eye would transfer without additional training to the other eye. It has been shown that a habit established with one portion of either retina in man is retained when any other part of the two retinas is used (Becher, 1911). In unpublished studies (see Levine, 1945*a*) contralateral transfer has been found in the rat for brightness and pattern discriminations and in the chicken for discrimination of two shades of gray. On the other hand, Beritov and Chichinadze (1937) found a lack of transfer of color discrimination in the pigeon. This was confirmed by Levine (1945*a*, *b*) for color and pattern discriminations involving the lower temporal part of the retina. Transfer was obtained, however, from the upper temporal part of the retina. Levine observed further that pigeons may learn a visual discrimination with only one eye, even though neither eye is blindfolded. The results on the pigeon show that interocular transfer cannot be assumed a priori for the lower vertebrates and that further information is needed.

What the presence or absence of interocular transfer may mean with respect to the neural basis of sensory equivalence, learning, and memory has yet to be determined. It was thought that the goby, a marine teleost, might be a good test animal for further analysis of the problem. The goby learns visual discrimination habits without excessive training; it can be effectively blinded for long periods with opaque eye caps; its optic nerves can be severed or its eyes transplanted with recovery of vision (Sperry, 1948, 1949); and its brain is simpler and amenable to more drastic surgery than that of warm-blooded vertebrates. Also this ani-

[1] The experiments were conducted at the Lerner Marine Laboratory of the American Museum of Natural History, at Bimini, British West Indies. They were aided by a grant from the Dr. Wallace C. and Clara A. Abbott Memorial Fund of the University of Chicago.

mal is hardy, easily secured and maintained, and, from the viewpoint of training, its relative immunity to affective disturbances from noise and movement in its surroundings and its tendency to remain on the bottom between trials constitute important advantages. As in other infra-mammalian vertebrates, the crossing of fibers in the optic chiasma is complete.

In the following experiments a group of these fish were taught a simple visual discrimination with a blinder on one eye. After the fish had been overtrained, the blinder was shifted to the opposite eye and the degree of transfer determined. In cases in which transfer was poor or lacking, the blinders were shifted once or twice more and the test performances for each eye compared. In a second series of fish, monocular performances were tested in a habit which had been acquired with both eyes uncovered.

MATERIALS AND METHODS

One of the gobies, *Bathygobius soporator* (Cuvier and Valenciennes) was used throughout. The specimens measured 24–43 mm. in standard length and were collected during February from tide pools on North Bimini. After a blinder had been placed on the right eye as described below, each fish was placed in a 2-gallon aquarium, 16 × 20 × 26 cm., with standing sea water that was changed approximately every 4 days. Two days were allowed for the fish to become hungry and accustomed to their aquaria before training was started.

These fish, instead of swimming about freely, spend most of their time clinging to the bottom and sides of the aquarium by means of their specialized pelvic fins. The training consisted of teaching the fish to swim to the higher of two stimulus objects presented simultaneously from above. The positive stimulus, a piece of conch, fish, or crab meat, approximately 5 mm. in diameter, was hung on stainless-steel wire, 35 mm. directly above a knotted wad of glass wool, or in other cases a piece of red rubber, about twice the size of the positive stimulus. There was an initial preference for the lower, larger object. At first the lures were set deep near the bottom and were left for several minutes until the fish overcame their timidity and explored the double lure. As training progressed the stimuli were presented at successively higher levels and were removed more quickly until, by the fifth day of training, merely dipping the lures into the water was sufficient to elicit an immediate response. Thereafter, the presentation was made randomly at various depths but, in the majority of trials, above the starting level of the fish.

If, in approaching the lures, the fish committed themselves in any way to an initial selection of the negative rather than the positive stimulus, even though an actual bite was not made, it was counted an error. The only punishment for an error was an abrupt withdrawal of the lures. When a correct trial was made, the lures were withdrawn gently after allowing the fish to nibble once or twice at the bait. An average of 30 trials was given per day after the fish had started to run well, 15 in the morning and 15 in the afternoon, with the individual trials in each series separated by intervals which varied from approximately 1/2 to 3 minutes.

Monocular blinding was accomplished by fitting an opaque cap of tantalum foil over one eye. The foil was first molded into a cup shape having approximately the curvature of the eye and then cut to fit the size of the eyeball. This cap was inserted between the eyeball and the free external cornea through an incision in the skin dorsal to the cornea just large

enough to permit passage of the cap. The diameter of these blinders was slightly less than that of the eyeball but greater than the longest dimension of the pupil, so that the latter was completely covered. The blinders did not impair eye movements and caused little or no mechanical inconvenience. In the majority of cases the incisions healed rapidly, sealing the blinders in place without infection or clouding of the cornea. In shifting the blinders from one eye to the other, the original incision was reopened, and the cap was pulled out and placed over the opposite eye in the same manner. These operations were performed with urethane anesthesia and always at night, in order that any affective disturbance might be dissociated as much as possible from the daytime training procedure.

Various measures were taken to rule out possible use of unintended nonvisual cues. Any dependence upon constant spatial cues was eliminated by presenting the bait randomly at different levels and in different parts of the aquarium. Use of olfactory cues was checked during the overtraining sessions by using a stale, washed-out piece of conch for bait and excessively flavoring the aquarium water with fresh conch tissue fluids. All the fish continued to run correctly under these conditions with no signs of confusion. Also when a wad of cotton of comparable size was substituted for the bait following the test trials, the fish continued to run directly to the cotton for as many as 7–12 consecutive trials. Upon presentation of the lures outside the glass walls of the aquarium on scattered trials during the overtraining sessions, the fish responded in the usual way and attempted to get the bait through the glass. With the lures outside the glass, it was not always possible to determine satisfactorily which one of the two stimulus objects was being aimed at, however, unless the approach was approximately horizontal. Only 3–4 trials of this latter sort were obtained per individual, but the manner in which the fish responded, as well as the bare scores in these tests through the glass, indicated that the habit was not dependent upon either chemoreceptor or lateral-line cues. The fact that the fish frequently approached the bait from above as well as from below in the later stages of training also tended to rule out lateral-line guidance.

Many fish with one eye blinded will easily get into the habit of approaching the bait with a partial turn toward the seeing side, a motor pattern which, in itself, might hinder performance with the other eye. Such turning was decreased by frequently placing the lures on a straight line in front of the fish. Especially in the final stages of overtraining, care was taken to be sure that the animals ran correctly with the bait directly in front. In the test trials the bait was always presented straight in front as close as possible to the mid-sagittal plane.

Near the end of the overtraining sessions each fish was netted, anesthetized with urethane, and manipulated as would be done in the course of an operation except that no surgery was performed. This was found to have no significant influence upon the training scores or upon the animals' readiness to run on the following morning.

RESULTS

Training was started with a group of 22 animals, 4 of which had to be discarded because they refused to run and a fifth because it failed in 12 days to reach a criterion of 17 correct out of 20 consecutive trials. The remainder attained this criterion in 3–7 days of training. The first 6 cases listed in Table 1 were trained with glass wool as the negative stimulus. In these the learning time averaged at least

2 days longer than in the others for which red rubber was used as the negative stimulus. The white color and general contour of the glass wool was very close to that of the bait, whereas, in the case of the rubber, color and form contrasts were present, in addition to the position and size differences.

After the learning criterion had been reached, the animals were overtrained for about 4 days or a minimum of 120 trials. The blinder was then shifted from the right to the left eye. During the 2 days preceding this shift of the blinder, the fish were running on the average about 85 per cent correct. The individual error scores for the final 25 trials immediately preceding the transfer of the blinder are shown in Table 1.

Although some of the fish responded readily on the morning following the shift of the blinder, others did not start to run again until the second or third day. There was no significant correlation, however, between this hesitancy to run and the degree of transfer of visual discrimination. One animal had to be discarded because its eye became infected and it refused to feed. In the remaining 16, a total of 25 trials was obtained with the left eye covered. The number of errors made by each is shown in the table. Apparently, transfer was almost complete in some animals (5, 9, and 12), but quite poor or negligible in others (2, 4, 7, 8, 11, 13, and 15).

In those fish in which transfer was poor or lacking, the blinder was shifted back again to the right eye. Case 11 became infected and refused to run. In the remaining 10 cases, 25 trials were obtained, and the scores all showed an abrupt, marked improvement to approximately the level attained previously with the right eye covered. It is possible that slowly developing infections, which became worse after the 25 trials had been obtained, served to increase the number of errors in cases 2 and 4. A third shift of the blinders back to the left eye was undertaken in Nos. 3 and 7; No. 3 again showed only poor transfer, whereas No. 7, in contrast to its earlier performance, this time exhibited good transfer.

In a second series of fishes trained for other experimental purposes, some incidental observations were obtained pertaining to the question of whether learning may be uniocular, as in the pigeon, even though neither eye is blinded during training. Fifteen animals were trained in the same way as above, except that both eyes were left uncovered. In all cases the negative stimulus was glass wool. Two cases did not run readily and were discarded. After the remaining 13 had been overtrained in 60–90 trials, a tantalum blinder was placed on the right eye, and 25 trials were given. In 6 of these cases the blinder was then switched to the left eye and 25 trials given with this eye covered. Finally, in these 6 and in 5 others the blinders were removed and 25

TABLE 1

NUMBER OF ERRORS MADE IN THE 25 TRIALS PRECEDING AND FOLLOWING TRANSFERS OF THE BLINDER IN SERIES I

Case No.	Eye Blinded			
	Right	Left	Right	Left
1	3	12	4	.....
2	5	20	11	.....
3	2	13	3	10
4	6	21	7	.....
5	5	6	.....	.....
6	4	8	.....	.....
7	3	19	5	5
8	2	18	2	.....
9	1	2	.....	.....
10	0	11	3	.....
11	2	22	.....	.....
12	5	6	.....	.....
13	3	18	4	.....
14	3	7	.....	.....
15	2	20	1	.....
16	2	10	4	.....

trials were given with both eyes uncovered. The use of the fish in this series for another experiment prevented further testing for monocular dominance. The error scores obtained are shown in Table 2.

The level of monocular discrimination was clearly too high in the group as a whole to support the supposition that learning and retention had been confined to one eye. Furthermore, high error scores in the last column of the table indicate that affective disturbance became an appreciable factor in this series in which the amount of overtraining had been less than in Series I. Accordingly, the impairment which can be attributed to unilateral blinding alone is probably somewhat less than indicated by the scores in the table.

TABLE 2

NUMBER OF ERRORS MADE IN 25 TRIALS PRECEDING AND FOLLOWING INSERTION AND REMOVAL OF THE BLINDERS IN SERIES II

Case No.	Eye Blinded			
	None	Right	Left	None
1	6	9	.....	4
2	0	15	11	1
3	3	8	9	7
4	3	16	.....	2
5	4	13	6	3
6	3	3	.....	.....
7	4	7	10	15
8	4	12	4	8
9	2	1	12	6
10	1	4	.....	.....
11	2	3	.....	2
12	3	3	.....	6
13	4	9	.....	2

DISCUSSION AND CONCLUSIONS

From the sudden drop in level of performance produced in the majority of cases by shifting the blinder from the untrained to the trained eye in Series I *plus* the consistent return to a high level of discrimination when the blinder was shifted back again to the untrained eye it may be inferred that interocular transfer does not take place in a complete and automatic fashion in these teleosts as it does in man. The untrained eye, in the majority of cases, is not always equally as good as the trained eye for a learned visual discrimination.

That the data might be accounted for alternatively in terms of generalized affective or motor disturbances associated with shifting the blinders seems implausible in view of the following: Affective disturbance would appear to be ruled out by the consistent improvement produced by the second shift of the blinders to the untrained eye and also by the apparent intrepidity with which many of the animals performed. Dependence upon a lateral bias in motor patterns was excluded by means already described. That the presence of the blinders over the eyes caused any regressive or atrophic changes in the visual system that might have been responsible for lack of transfer seems improbable. Some animals showed good transfer on the day after the blinders were shifted, while others that did not respond until the second and third days failed to show transfer.

On the other hand, from the high degree of transfer that did take place in a minority of cases it may also be inferred that interocular transfer is by no means impossible in these fish. The question arises in this regard as to whether the apparent interocular transfer in these instances might not have been based upon nonvisual cues. Certainly, many aspects of the habit were not visual and accordingly would be expected to survive the shift of the blinders. However, that component of the habit which involved the initial localization of the lure in space is something for which vision was indispensable. Gobies which have been trained to rise to such a lure are no longer

able to locate it after bilateral blinding, even though, with olfactory excitation, they may dart about in obvious search for it. This conditioned response to swim directly to the lure upon its presentation, exclusive of any discrimination between its positive and negative portions, transferred in varying degree in all cases, even in those animals in which the discriminatory component failed to transfer.

That transfer of the discrimination itself might have been dependent upon olfactory and lateral-line rather than upon visual cues seems to be discounted by various considerations already mentioned to which the following may be added: The direct course taken in the approach to the lure and the speed of the proach when the animals were running correctly indicated that, in general, the discrimination had already been made before the fish got close enough to use any olfactory or lateral-line cues. Slow, hesitant approaches, in which the fish did not commit themselves until they were close to the lure, were correlated with poor scores rather than with good scores. It was not uncommon for a fish which was running poorly to approach to within 2–3 cm. of the lure and, after hovering in this position for some time, to strike finally at the glass wool or rubber. Although absolute proof is lacking that a combination of lateral-line and chemical cues may have been responsible for the transfer, the evidence, on the whole, is against such an interpretation.

In the course of the training period the majority of the blinders slipped a little from their original position. In some cases this was sufficient to allow a thin crescent of peripheral vision, usually downward. However, there was no correlation with this accidental peripheral vision in the covered eye and the extent of transfer. In none of those in which transfer occurred was the peripheral vision upward or forward. In two of them there was no peripheral vision at all in the covered eye. Among the group that did not transfer, on the other hand, were two cases with slight peripheral vision upward and forward. It should be recalled that the blinders moved with the eyeball, and therefore a thin opening under the edge of the blinder could not be utilized to the extent that is possible with external blindfolds of the type used on birds and mammals.

In summary, the results in Series I point to the conclusion that monocularly acquired visual discrimination habits are subject to contralateral transfer in the goby, i.e., the organization of this teleost brain does not preclude interocular transfer. At the same time, however, it must also be concluded that the neural mechanisms are not so well developed that they consistently insure complete and automatic transfer in all instances, as in man.

It was not possible to correlate the lack of transfer with any particular factor, such as apparent timidity or slowness in approaching the lures, extent of overtraining (within the limits of the experiments), slowness of learning, etc. Nor was there anything to suggest that those fish which showed interocular transfer had learned the discrimination with a different part of the retinal field from that used by those in which transfer failed to occur. Further evidence on this and other points would be desirable before trying to assess the implications of the data for problems concerning the neural basis of visual learning, memory, and sensory equivalence.

In Series II the degree of impairment of the binocularly acquired habit caused by the unilateral blinding was much too small for the group as a whole to be compatible with the assumption that the discrimination had been learned exclusively

by one dominant eye with no interocular transfer. If learning and retention had been confined to one eye, approximately half the fish should have shown severe or complete loss of correct discrimination when the right eye was blinded, and the remainder ought to have shown similar loss when the other eye was blinded. Possible influences upon the error scores caused by affective or other generalized disturbances associated with insertion of the blinders would serve only to strengthen the foregoing inference.

SUMMARY

1. Inserted blinders of tantalum foil were devised for monocular training of visual discrimination habits and the testing of interocular transfer in fishes.

2. Sixteen gobies with a blinder on the right eye were trained against an initial preference to swim to the smaller, higher, and less brightly colored of two lures presented simultaneously. Controls were run to rule out the use of nonvisual cues.

3. After the fish had been overtrained 4 days or a minimum of 120 trials, the blinder was shifted to the opposite (left) eye. Retention tests revealed excellent or good interocular transfer in 5 of the 16 cases. Lesser degrees of transfer were evident in 4 cases, while in the remaining 7 the transfer was poor or negligible. When the blinder in these last 11 cases was shifted again to the untrained (right) eye, the scores promptly underwent a marked improvement to approximately their previous level.

4. An additional shift of the blinder to the trained (left) eye in 2 cases again caused deterioration of the habit in 1 of them. In the other, however, in contrast to the earlier result in the same individual, excellent transfer was manifest.

5. In a second series of 13 fish, monocular performances on visual discrimination habits learned with both eyes uncovered indicated that learning and retention had not been confined to one dominant eye as found in some earlier experiments with pigeons.

6. The results seem to support the conclusion that the brain organization of this teleost fish permits interocular transfer, but that, at the same time, the neural mechanisms involved are not so well developed that good transfer is automatically assured in all instances.

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